

PREDATORY BEHAVIOR OF THREE SPECIES OF SAC SPIDERS ATTACKING CITRUS LEAFMINER

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ABSTRACT. The predatory habit of three species of sac spiders, *Chiracanthium inclusum*, *Hibana velox*, and *Trachelas volutus*, on citrus leafminer, *Phyllocnistis citrella*, was investigated. Observation of spider activities during the photophase and the scotophase confirmed that these three species of sac spiders are nocturnal. They detect their prey by sensing vibrations of the substrate induced by the concealed prey. Movements of *P. citrella* larvae and prepupae appear to create vibrations of the leaf substrate, which then serve as cues for the spiders to locate them. The searching and prey capture behaviors of these spiders are discussed. Two methods of prey attack were exhibited. In one method, the spider punctures the mine, immobilizes the larva and then bites it and sucks the larval body fluid. In the second behavioral pattern, the spider makes a slit in the mine, uses its forelegs to pull the larva or prepupa out of the mine, holds the prey securely, and finally bites it and regurgitates digestive juices into the prey and ingests the pre-digested liquid tissue.

The three species of sac spiders were found to start feeding on *P. citrella* larvae during the 2nd instar stage. Consumption increased as they developed to later instars. Maximum consumption for all species was recorded at the 4th instar. Although *C. inclusum* and *T. volutus* can complete their life cycle with *P. citrella* as their only food, *H. velox* was not able to develop to the adult stage. Results obtained from this study provide useful data to better understand the role of sac spiders in the overall management of *P. citrella*.

Keywords: Nocturnal, prey capture, feeding stage, *Phyllocnistis citrella*, sac spiders

The citrus leafminer, *Phyllocnistis citrella* Stainton (1856) (Lepidoptera, Gracillariidae) has become an important pest of *Citrus* spp. in Florida since its introduction in 1993 (Knapp et al. 1995). The larvae of *P. citrella* mine in leaf tissues of any citrus and related species (Heppner 1993). *Phyllocnistis citrella* larval feeding results in citrus plants with distorted and reduced young shoots. Severe pressure from *P. citrella* causes decrease in yields and quality (Knapp et al. 1995; Heppner 1995; Bugeous & Constantin 1995). Although many insect parasitoids of this pest have been recorded (Heppner 1993), little attention has been directed towards predators of the larvae. Predatory arthropods are believed to make an important contribution to the mortality of *P. citrella* (Zhao 1989; Zhang et al. 1994; Argov & Rosler 1996; Browning & Peña 1995; Amalin et al. 1995; Peña & Subramanian unpubl.). In Israel, spiders were observed in the field to prey upon *P. citrella* (Argov & Ros-

ler 1996). Likewise, in south Florida, various species of spiders were considered important in reducing peak populations of *P. citrella* (Browning & Peña 1995; Amalin et al. 1995). Feeding tests on 14 commonly encountered spider species in lime orchards in Homestead, Florida confirmed that the three species of sac spiders, *Chiracanthium inclusum* (Hentz 1847) (Clubionidae), *Hibana velox* (Becker 1879) (Anyphaenidae), and *Trachelas volutus* Gertsch 1935 (Corrinnidae), fed on *P. citrella* larvae and, in some cases, on prepupae (Amalin 1999). Apparently these species of spiders are able to detect and attack the larvae through the leaf epidermis. This phenomenon of search and extraction of a cryptic food source has not been reported in this group of spiders. Because of this specialized feeding behavior, these spiders may prove to be important predators of *P. citrella*. Study of the predatory habits of these spiders on citrus leafminer is of paramount importance to better

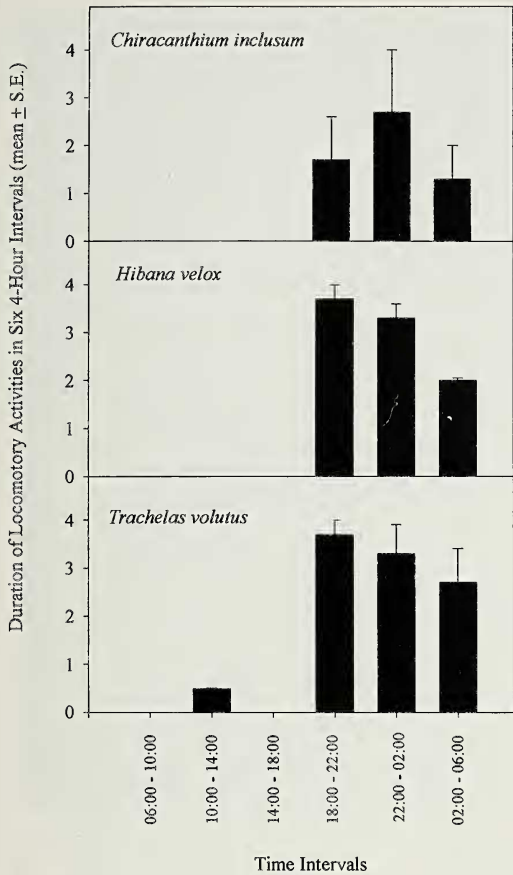


Figure 1.—Duration of locomotory activities in three species of sac spiders measured in six 4-hour intervals. Lights turned off at 1800 h.

understand the potential of these predators as a component of the natural enemy complex of *P. citrella*.

In this paper, investigations of the predatory behavior of three species of sac spiders (*C. inclusum*, *H. velox*, and *T. volutus*) attacking *P. citrella* is reported. The main objectives of this study were to determine the time of feeding activity, to investigate the predation strategy, and to identify the developmental stages of spiders that feed most actively on *P. citrella*.

METHODS

Sources of test organisms.—Egg sacs of *C. inclusum*, *H. velox*, and *T. volutus* were collected from citrus orchards in the vicinity of Homestead, Florida. Egg sacs were identified based on descriptions by Amalin (1999). They were brought to the laboratory and

maintained in the incubator at 27 °C, 80% RH, and 12:12 h photoperiod and reared on an artificial diet (Amalin 1999). Laboratory-reared 4th instar spiders were used for the experiments to determine the time of feeding activity and predatory strategy. *Phyllocnistis citrella* larvae were collected from a culture on lime (*Citrus aurantifolia*) plants maintained in the greenhouse. Voucher specimens are deposited at the Tropical Research and Education Center, Dept. of Entomology, Homestead, Florida.

Time of feeding activity.—Feeding times of the three sac spiders were determined from observations over a 24 hour period. A plastic petri plate (10.5 cm diameter × 2.0 cm high) was used as the observational arena. Lime leaves with five *P. citrella* larvae within the serpentine mines were placed in each petri plate. The number of *P. citrella* exposed to the spider is based on the result of the predation experiment previously conducted (Amalin 1999), in which a ratio of one spider to 10 *P. citrella* larvae gave an average of 5.3 *P. citrella* larvae consumed.

A single 4th instar spider was placed in each arena that was lined at the bottom with moistened filter paper to retain the freshness of the leaves. The test spiders were fed with artificial diet (Amalin et al. unpubl.) for 24 h before transferring to each petri plate; in this way the hunger level is controlled. All the petri plates were placed in an incubator with constant temperature (27 °C), relative humidity (80%), and a 12:12 h photoperiod. These were the same conditions under which spiders have been previously reared. Observations of spider activities were made every 15 min during the photophase and during scotophase by the use of a portable red light with an intensity of 5.0 Lux. Some arthropods (Borror et al. 1992; Jackson 1977) cannot recognize red light. Thus, red light is used to observe their nocturnal activities. The set-up was repeated three times on separate dates for each of the three spider species. The circadian rhythm of locomotory activity was observed to determine if they are diurnally or nocturnally active animals. Duration of movement in six 4 h intervals (0600–1000, 1000–1400, 1400–1800, 1800–2200, 2200–0200, 0200–0600) was noted.

Predatory strategy.—Spider activities were recorded by videotaping, using a video



Figure 2.—*Chiracanthium inclusum* touching or sensing the *Phyllocnistis citrella* larva by its hindleg. Arrow shows the *P. citrella* larva still within the serpentine mine.

time lapse cassette recorder (Panasonic Model AG-6730). A television monitor (Sony Trinitron) and a video camera (Javelin Chromachip V, Model JE-3662RGB) were hooked-up to the video recorder. The video camera was held on top of a tripod. The three species of sac spiders included in this observation were placed separately in a small petri plate (3.5 cm diameter \times 0.5 cm high). The petri plate was provided with five *P. citrella* 2nd instar larvae still within their serpentine mines. The petri plate was positioned under the tripod. The exact position of the petri plate was determined by looking at the television monitor. The video machine was set to 16 h recording continuously. The videotaping was conducted in a room with lights off from 1800 h until 0700 h the next day. To have a clear view of the predatory activity under total darkness, red lights (5.0 Lux intensity) were provided under the tripod. The set-up was repeated five times for each species. After videotaping, each tape was viewed and the following data were gath-

ered: retreat period (no locomotion, no body movement, the spider remained inside the retreat nest); searching time (locomotory activity); and handling time (period from start of attack until prey was consumed). The mean and standard error of the time spent for each activity were calculated. The number of *P. citrella* consumed was counted under a microscope the following morning and the average number of *P. citrella* consumed was calculated. The mean difference for each parameter was compared using Duncan Multiple Range Test (DMRT) (SAS 1989).

Active feeding stages.—to determine spider developmental stages capable of feeding on *P. citrella*, the three species of spiders were reared from the 2nd instar to the adult stage using *P. citrella* larvae their sole food source. Ten *P. citrella* 2nd instar larvae within the serpentine mines were placed in each petri plate (10.5 cm diameter \times 2.5 cm high). Individual 2nd instar spiders were introduced into each petri plate. Ten spiders of each spe-

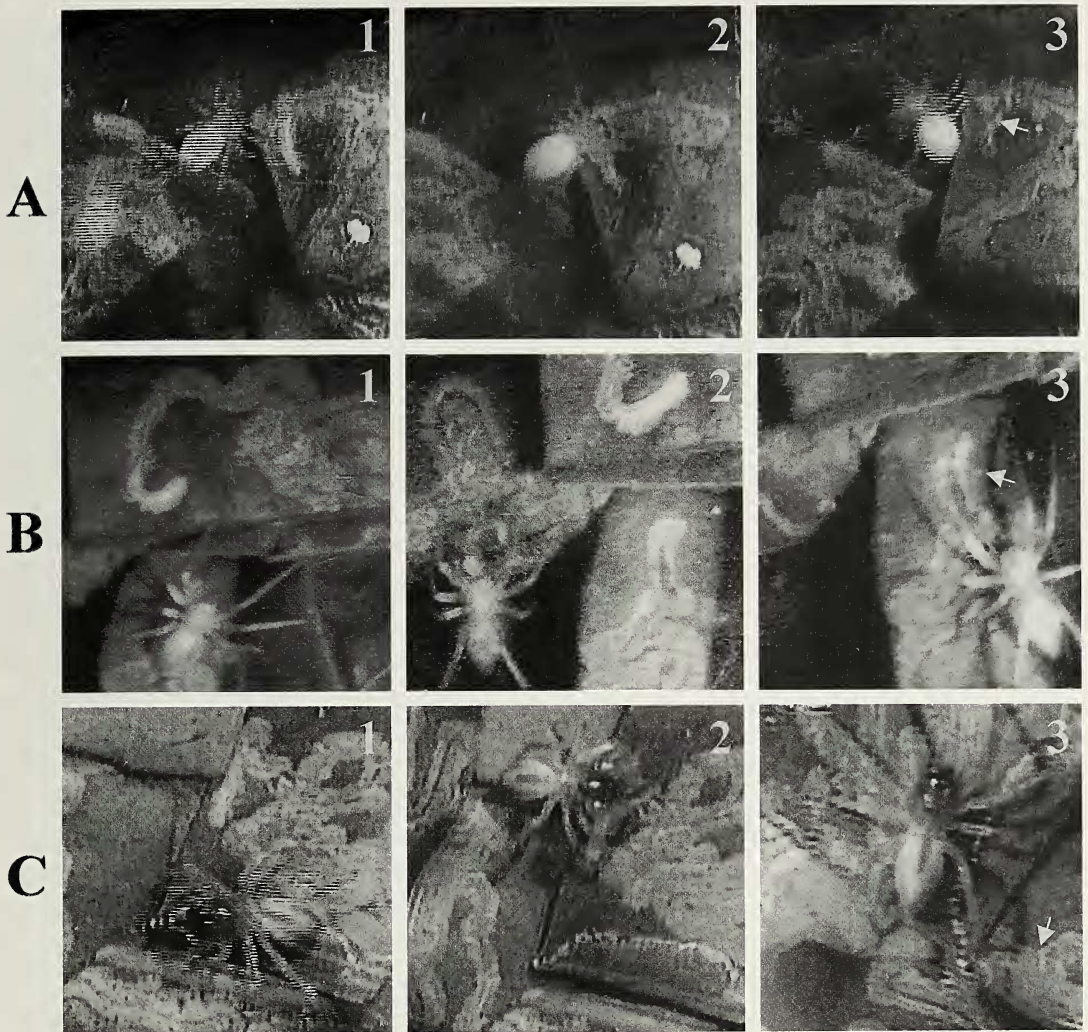


Figure 3.—Predation sequence of (A) *Chiracanthium inclusum*, (B) *Hibana velox*, (C) *Trachelas volutus*—searching (1), feeding (2), and after feeding (3). Arrows in A3, B3, and C3 show the empty serpentine mines after spider feeding.

Table 1.—Duration of time for predation activity and the percent *Phyllocnistis citrella* consumption in 24 hours by the 4th instar spiderlings of *Chiracanthium inclusum*, *Hibana velox*, and *Trachelas volutus*. All figures are mean \pm S.E. of five replications. Means in each column with the same letters are not significantly different according to DMRT.

Spider species	Searching time (min)	Handling time (min)	% <i>P. citrella</i> consumption
<i>Chiracanthium inclusum</i>	22.8 \pm 7.6 a	10.8 \pm 2.5 a	60.0 \pm 24.0 b
<i>Hibana velox</i>	8.8 \pm 4.8 b	11.3 \pm 5.7 a	64.0 \pm 16.0 b
<i>Trachelas volutus</i>	5.5 \pm 1.2 b	6.5 \pm 4.7 a	90.0 \pm 11.0 a

Table 2.—Percent *Phyllocnistis citrella* larval consumption by the different instars and adult stage of *Chiracanthium inclusum*, *Hibana velox* and *Trachelas volutus*. All figures are mean \pm S.E. of 10 replications. Data for immature stages of female and male spiders for all species are pooled.

Species	Immature (instar) stage							Adult	
	2nd	3rd	4th	5th	6th	7th	Female	Male	
<i>C. inclusum</i>	38.2 \pm 4.1	44.8 \pm 4.1	57.0 \pm 7.0	27.9 \pm 7.6			37.0 \pm 15.0	34.3 \pm 17.0	
<i>H. velox</i>	25.6 \pm 3.0	46.2 \pm 6.0	70.5 \pm 6.5	57.2 \pm 11.4	35.6 \pm 14.0	8.4 \pm 8.4			
<i>T. volutus</i>	58.7 \pm 9.7	47.2 \pm 5.4	61.3 \pm 11.8	45.3 \pm 14.6			70.7 \pm 7.6	65.3 \pm 9.6	

cies were included in the experiment. Dead *P. citrella* larvae were counted every other day, and after the mortality reading, new citrus leafminer larvae were added to each petri plate to keep the number of *P. citrella* constant. The molting period was recorded for each spider to determine the developmental stages.

RESULTS

Time of feeding activity.—The mean duration of locomotory activity for each species was grouped in six 4 hour time intervals. Our observations confirmed that *C. inclusum*, *H. velox*, and *T. volutus* are all active nocturnally (Fig. 1). The onset of movement for *C. inclusum* and *H. velox* was at the beginning of interval 4, which was about one hour into the scotophase. One out of the three *T. volutus* showed some locomotory activity 4 h into the photophase. The observed daytime activity of this individual *T. volutus* was very brief, lasting only for two consecutive 15 min observation periods, and was followed by a retreat period of about 7 hours. The peak of locomotory activity for the three species occurred during intervals 4 and 5. The locomotory activity was reduced at the end of interval 6.

Predatory strategy.—The pattern of the prey capture sequence was similar for the three species of sac spiders. During the searching period, the spiders would move about and then stop for a while as if to localize the source of the vibration. Immediately upon touching the prey with its legs (Fig. 2), the spider would turn very rapidly toward the prey and grasp it. Figure 3 shows the predation sequence of these three species of sac spiders. Two behavioral patterns of prey attack were exhibited by the three species of sac spiders. In one strategy, the spider punctured the mine, immobilized the larva, bit it and sucked the larval body fluid (Fig. 3A & C). In the second behavioral pattern, the spider made a slit on the mine, and then used its forelegs to pull the larva or prepupa out of the mine (Fig. 3B). The first gentle touch with the forelegs, probably aided by special sensory hairs on the forelegs, was quickly changed into a powerful grip. Only after the prey has become immobilized by the venom does the spider begins to feed (chew and exude digestive juice).

The searching time or the time to locate the prey differed among the three species. An av-

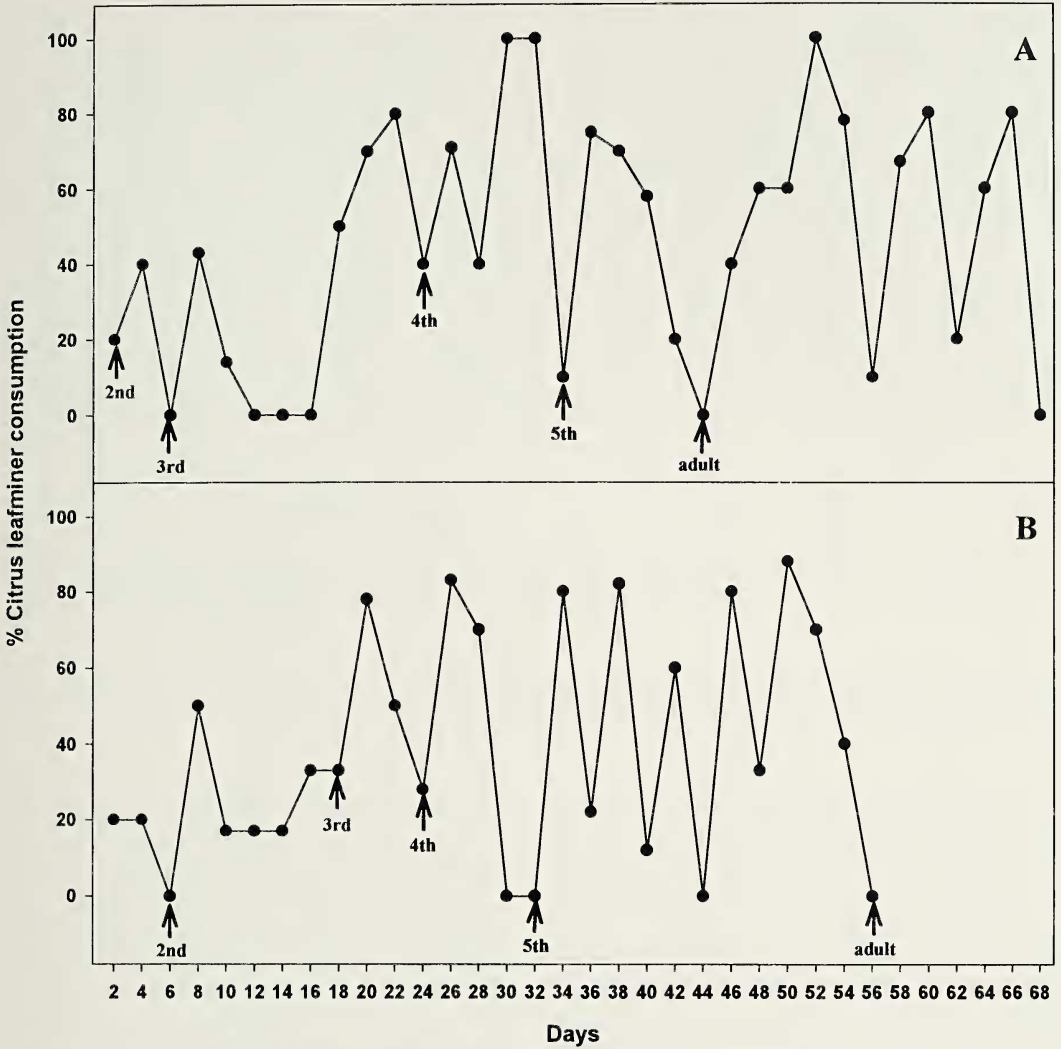


Figure 4.—Development of (A) female and (B) male *Chiracanthium inclusum* raised using *Phyllocnistis citrella* larvae. Arrows refer to molt when a new instar stage begins.

erage of 5.5, 8.8, and 22.8 minutes was spent on prey location by *T. volutus*, *H. velox*, and *C. inclusum*, respectively (Table 1). It took *C. inclusum* significantly longer time to locate the prey than *T. volutus* and *H. velox*. There was no significant difference in the time spent by the three species of spiders to handle and feed on *P. citrella* (Table 1). Moreover, it was observed that *C. inclusum* and *H. velox* moved more frequently in the observational arena than *T. volutus* did. The postfeeding (resting) period for *C. inclusum* and *H. velox* was extensive, while that of *T. volutus* was brief. These behavioral differences may explain why the average percent *P. citrella* consumption

was significantly higher for *T. volutus* (90%) than for *C. inclusum* (60%) and *H. velox* (64%) (Table 1).

Active feeding stage.—Our observations revealed that *C. inclusum*, *H. velox*, and *T. volutus* started to feed on *P. citrella* larvae as 2nd instar spiders. The percent *P. citrella* consumption for the three species of sac spiders differed among the different instars and adult stage (Table 2). Maximum consumption was recorded at the 4th instar for all species. This stage has progressed midway to the adult stage, and they feed voraciously to meet the energy and nutritional demands of final maturation. *Chiracanthium inclusum* and *T. vol-*

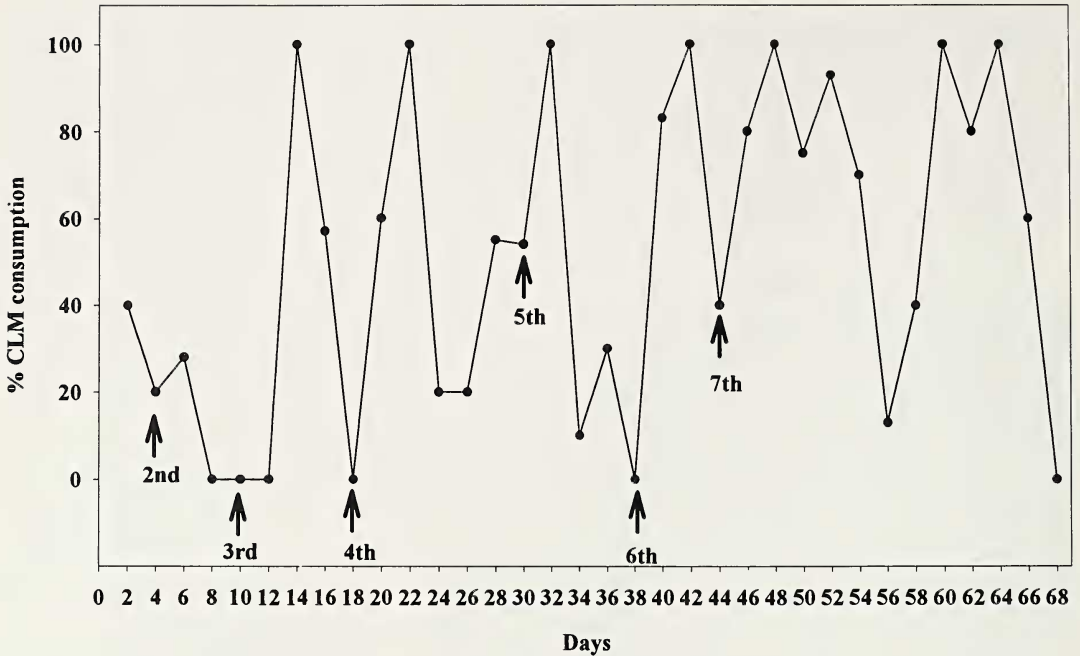


Figure 5.—Development of *Hibana velox* raised using *Phyllocnistis citrella* larvae. Arrows refer to molt when a new instar stage begins. The female and male immature stages are pooled.

utus can complete their life cycles with *P. citrella* as their only food source (Table 2); however, *H. velox* was unable to complete its life cycle by feeding solely on *P. citrella* (Table 2). For all of the species, feeding slowed down and sometimes stopped for 1–2 days before molting and then resumed after the molt. Individual spiders had different time intervals from one molting period to the next. Figures 4–6 show an example of the development pattern of the three species of spiders from the 2nd instar to the adult stage.

DISCUSSION

The 24 hour observation periods revealed that *C. inclusum*, *H. velox*, and *T. volutus* are generally nocturnally active animals. The brief locomotory activity of *T. volutus* during the daytime could mean that *T. volutus* may be also active for short times during the day. This could be verified by doing more daytime observations. The activity of most wandering spiders is correlated with a particular light level (Seyfart 1980). In the field we rarely see these spiders in the daytime unless we venture to look at their retreat nests. These spiders have poor vision. Their eyes are simple (Land 1985); and they rely little, if at all, on visual

cues in prey capture sequences. They possibly detect their prey through vibration of the substrate where the prey is concealed. The constant movement of *P. citrella* larvae while feeding on tissues under the leaf epidermis probably creates the vibrations of the leaf substrate (I. Jackson pers. commun.). It appeared then that such vibrations serve as the cue for the spiders to locate the position of the larva or prepupa of *P. citrella*. The wandering spider *Dolomedes* sp. can distinguish between the ripples caused by the wind and the surface vibrations generated by an insect (Bleckmann & Rovner 1984). This may be true also for *C. inclusum*, *H. velox*, and *T. volutus*. The surface vibration produced by the movement of *P. citrella* larval feeding probably has a characteristic level of frequency and amplitude that can be distinguished by the sac spiders. However, this remains to be verified.

The prey capture sequence exhibited by *C. inclusum*, *H. velox*, and *T. volutus* followed the entire prey capture stages summarized by Foelix (1996) for wandering spiders. For this group of spiders, the main signal for prey capture is mechanical vibration. Once the prey is located, the spider grasps the prey with the

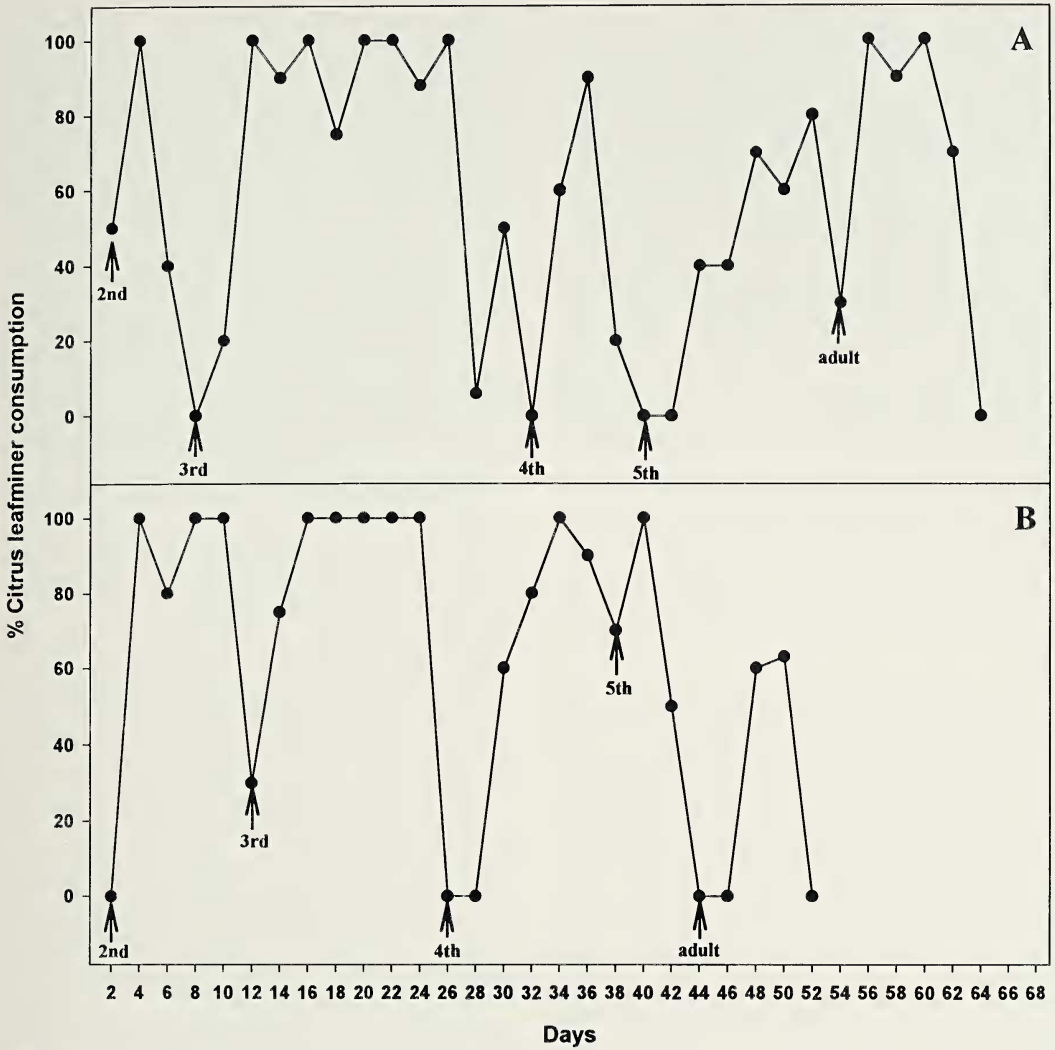


Figure 6.—Development of (A) female and (B) male *Trachelas volutus* raised using *Phyllocnistis citrella* larvae. Arrows refer to molt when a new instar stage begins.

tips of the front legs. Rovner (1978) reported that for the wandering spider *Cupiennius* sp. the forelegs are able to further secure their hold by means of the adhesive hairs or scopulae on the tarsi. This may also be so for *C. inclusum*, *H. velox*, and *T. volutus* since these three species of sac spiders possess tarsal scopulae and dense claw tufts (Roth 1993; Edwards 1958; Platnick 1974). After the spider secured its hold, the prey was quickly pulled toward the spider's body. Thereupon the chelicerae of the spider's fangs moved apart and were inserted quickly into the nearest part of the victim's body. Immediately after the bite, the tips of the legs released their grip and the

prey was held in the air only with the chelicerae. The behavior appears to minimize any danger to the spider from the prey. Holding the prey aloft is advantageous to the spider because the victim cannot apply any force against the substrate to free itself.

The three species of spiders started to feed on *P. citrella* larvae during their 2nd instar. This is not surprising since spiders, after molting into the 2nd instar stage, are generally found to be self-sufficient (Foelix 1996). At this stage, they have developed their sensory hairs, their legs are equipped with the typical claws, they have bulging eyes, and their mouthparts are already differentiated suffi-

ciently for capturing and feeding on prey. Then, the consumption increases, as they develop to later instar stages. During the intermolt intervals spiderlings require ample food to enable them to develop into the next stage (Foelix 1996). However, feeding slowed down before molting. This occurs naturally in all spiders. Foelix (1996) stated that most spiders that were preparing to molt withdraw into their retreat for several days and stop feeding. The success of rearing *C. inclusum* and *T. volutus* from egg to maturity using *P. citrella* alone as the source of food is an indication that these spiders do not require a varied food supply as compared to *H. velox*. Evidently, *H. velox* requires a varied food supply to complete its developmental cycle. Greenstone (1979) and Uetz et al. (1992) reported that certain spiders must feed on a variety of insect prey species to obtain the optimum nutrition for survival. This may also hold true for *H. velox*.

The results obtained from this study provide useful data to better understand the role of spiders in the overall management of *P. citrella* populations. Detailed observations on the predatory behavior of these three species of sac spiders showed that they exhibited a specialized feeding behavior in which they can search and extract a cryptic food source. This predatory behavior may merit their consideration as important predators of *P. citrella*, and they perhaps should be considered in the natural enemy complex of *P. citrella*. This potential can be realized only if these beneficial predators are fostered by orchard care practices.

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